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MORPHOLOGY OF CERATOZAMIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 153

CHARLES J. CHAMBERLAIN

(WITH PLATE I AND SEVEN FIGURES)

Southern Mexico, with its three genera of cycads (*Dioon*, *Ceratozamia*, and *Zamia*), is the principal cycad region of the western hemisphere. Two of these genera, *Dioon* and *Ceratozamia*, may be confined to Mexico. Occasional reports indicate a wider distribution, but both genera are so commonly cultivated in parks, both in Mexico and farther south, that descriptions, even when supported by specimens, would need the addition of observation in the field before habitats could be established. The first two descriptions of *Dioon spinulosum*, by DYER (1) and by EICHLER (2), were based upon cultivated specimens, and in the localities cited, Progreso and Cordoba, the species does not occur except in cultivation.

Ceratozamia has been reported beyond Mexico, but whether from observation in the field or from cultivated specimens, is uncertain. It grows wild at Chavarrillo, where it is associated with *Dioon edule*, but the plants are only seedlings with 2 or 3 leaves, except on Monte Oscuro, where there are some specimens large enough to bear cones. Between Jalapa and the extinct crater of Naolinco is a beautiful valley, and on the Jalapa side of the mountains which rise from this valley, large fruiting plants of *Ceratozamia* are abundant, but are limited to a rather narrow vertical

distribution, the altitude of which was not determined. Most of my material came from this region, largely from the hacienda of Señor LUIS CARAZA.

It is a pleasure to acknowledge my indebtedness to Governor TEODORO A. DEHESA and Mr. ALEXANDER M. GAW. During my first trip to Mexico in 1904, I failed to find any *Ceratozamia*, except a few seedlings at Chavarrillo, but after I had returned to Chicago, Governor DEHESA stationed an officer near cultivated plants in the park at Jalapa, and the officer questioned country people until he found one who knew where the plant grew wild. The region was the mountainous slope of the valley just referred to. After that, cones were easily secured, and for six years Mr. GAW has sent cones at all seasons, until the series is very complete. Besides, I have been able to visit the valley myself, first in September 1906, and later in March 1908. On the latter trip, and again in September 1910, I found *Ceratozamia* in the mountains across the Papaloapan River at Tuxtepec, but the plants were rather small and bore no cones.

The plants in the valley, near Jalapa, I identified as *Ceratozamia mexicana*. There is considerable variation, aside from that which the leaves of cycads present at various stages in the growth of the plant, the variation appearing even in the cones, which show less variation than the vegetative structures.

In habitat *Ceratozamia* differs decidedly from *Dioon edule*, which grows in the open, exposed to blazing sunlight, while *Ceratozamia* is found in densely shaded places. The difference in light will be appreciated from the fact that a photographic plate which would be well exposed for *Dioon* in one-fifth of a second would require three minutes exposure for *Ceratozamia*. The *Ceratozamia* associated with *Dioon* at Chavarrillo always appeared stunted, with one, two, or three leaves, except on Monte Oscuro, where it is shaded by a dense growth of shrubs. Although *Ceratozamia* is not found in wet situations, it is associated with a luxuriant vegetation, while *Dioon edule* and the plants associated with it are xerophytic. The habitat of *Ceratozamia* resembles that of *Dioon spinulosum*, but the latter plant does not occur in the Jalapa region. In the Tuxtepex region *Ceratozamia* appears before the *Dioon* locality is reached, but I did not find the two growing together.

The trunk and leaves

The trunk of *Ceratozamia mexicana* seldom reaches 2 meters in length. It is rather slender, has an armor of persistent leaf bases,

FIG. 1.—*Ceratozamia mexicana* growing on a steep mountain side opposite Naolinco, near Jalapa.

and is often curved or prostrate. This habit is doubtless due to the fact that so many plants grow on steep slopes (fig. 1), for the apex

is always vertical. As in *Dioon*, the foliage display consists of two crowns, the latest fresh and bright green, while the previous one has a dull green color, or may appear pale or gray on account of the numerous small lichens which almost invariably incrust the leaves of the second crown. Few plants have more than 10 leaves in a crown, so that the foliage display of a large plant consists of about 20 leaves. On the larger plants the leaves are 1.5–2 meters in length and have 40–50 leaflets on each side, the leaflets measuring about 50 cm. in length and 2 cm. in width. The variation in the leaves of plants of different ages is readily seen from the fact that the first leaf of a seedling usually has 4 leaflets, sometimes only 2, and that these early leaves are shorter, thinner, and narrower than the leaves of old plants. Differences may also appear in the margins of the leaflets and in the spines on the lower part of the petiole, so that identifications based upon the leaf alone must be regarded with some suspicion.

A section of the adult stem shows that it is strictly monoxylic, with a very narrow zone of wood showing no growth rings (3).

The strobili

Strobili are not abundant, and occasionally Mr. GAW had difficulty in securing them. When very young, the ovulate and staminate strobili have the same general appearance, but even then they may be distinguished superficially by the much larger number of sporophylls on the staminate strobili, and by the fact that the staminate strobilus is somewhat conical, while the ovulate is cylindrical. At maturity the staminate strobilus is quite pointed, while the ovulate is very evenly cylindrical and is much larger.

THE STAMINATE STROBILUS

The staminate strobilus reaches its full size and sheds its pollen about the middle of March. The largest staminate strobili are about 20 cm. in length, but the average length is not more than 15 cm. A typical staminate strobilus is shown in fig. 2. The sporophylls are somewhat wedge-shaped, distinctly stalked, and are tipped by the two horny spines which give the name to the

genus. The sporangia are crowded over the entire abaxial surface of the sporophyll, with only a slight indication of any division into two groups by a sterile line through the center (fig. 3). The sori consist of three or four sporangia, with some two's and occasionally a single sporangium, the single sporangium being found more frequently at the top and bottom of the strobilus. The soral character is not always evident in a surface view, but is rather distinct after the pollen has been shed (fig. 3, *c*), and is easily seen by removing the sporangia or by examining sections (figs. 3, 4). Dehiscence begins in the peripheral sporangia of the sporophyll and progresses toward the axis of the cone, as shown in fig. 3, *b*. As in *Dioon edule*, the wall of the sporangium is thin at the sides and thicker at the top, with a thick-walled outer layer of cells and thin-walled cells between this and the sporogenous tissue. The dehiscence is marked by two rows of thin-walled cells which contrast sharply with the thick-walled cells of the rest of the outer layer. The cells of the outer layer are elongated parallel to the dehiscence, so that in a section at a right angle to the dehiscence they are almost square in outline (fig. 5), while in a sec-

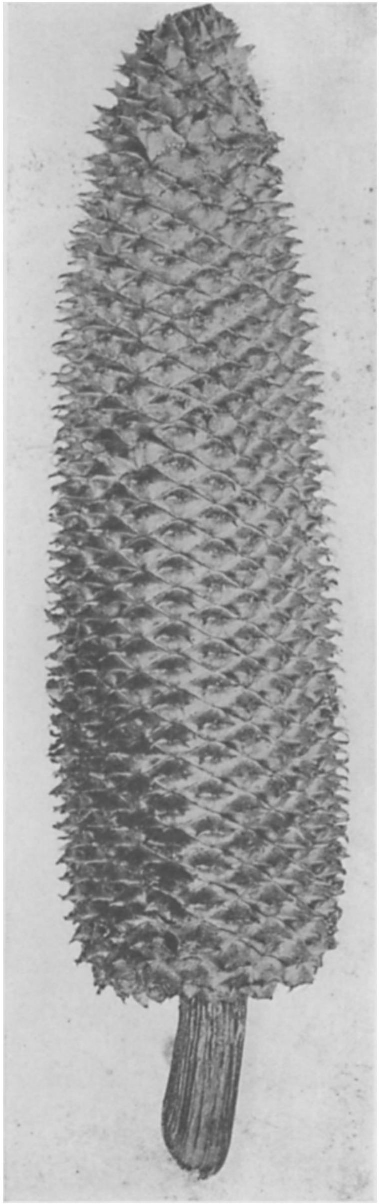


FIG. 2.—Staminate strobilus; $\times \frac{2}{3}$.

tion parallel to the dehiscence the length is several times as great as the breadth.

THE OVULATE STROBILUS

The ovulate strobilus is cylindrical in outline, and when mature is green and smooth. There is such variation in the size and general appearance of the strobilus that if one considered only the extremes he could easily describe new species. What may be regarded as extremes in the appearance of large cones is represented in figs. 6 and 7. The largest cone noted in several year's collections was 33.5 cm. in length and 11 cm. in diameter, and the smallest measured 21×8.5 cm. The average size is about 26.3×9.7 cm.

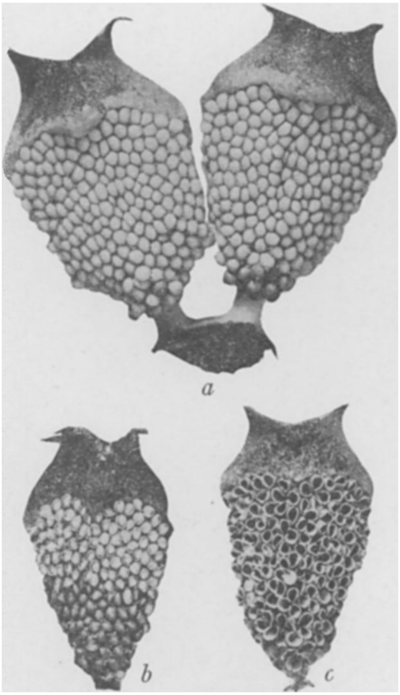


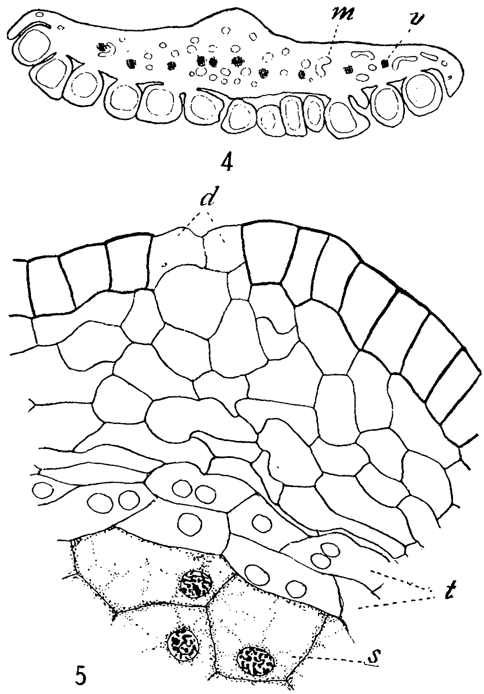
FIG. 3.—Staminate sporophylls: *a*, before dehiscence; *b*, dehiscence has taken place in the upper half but not yet in the lower; in *c*, nearly all the sporangia have shed their pollen; ×2.

The sporophylls appear to be arranged in vertical rows, and the number of sporophylls can be determined with considerable accuracy by counting the number of rows and number of sporophylls in a row, but the arrangement is s t r i c t l y s p i r a l. The lowest number of sporophylls observed was 72, in 8 rows with 9 in a row; and the highest number was 182, in 14 rows with 13 in a row; an average computed from 12 well developed cones was 11 rows with 11 in a row. The number of sporophylls, therefore, varies from 72 to 182, with 121 as an average; and the number of ovules varies from 144 to 364, with an average of 252, since each sporophyll bears two ovules.

The two hard spines or horns, which are similar to those on the microsporophyll, are always conspicuous, and they are so stiff and sharp that they make a large cone an uncomfortable object

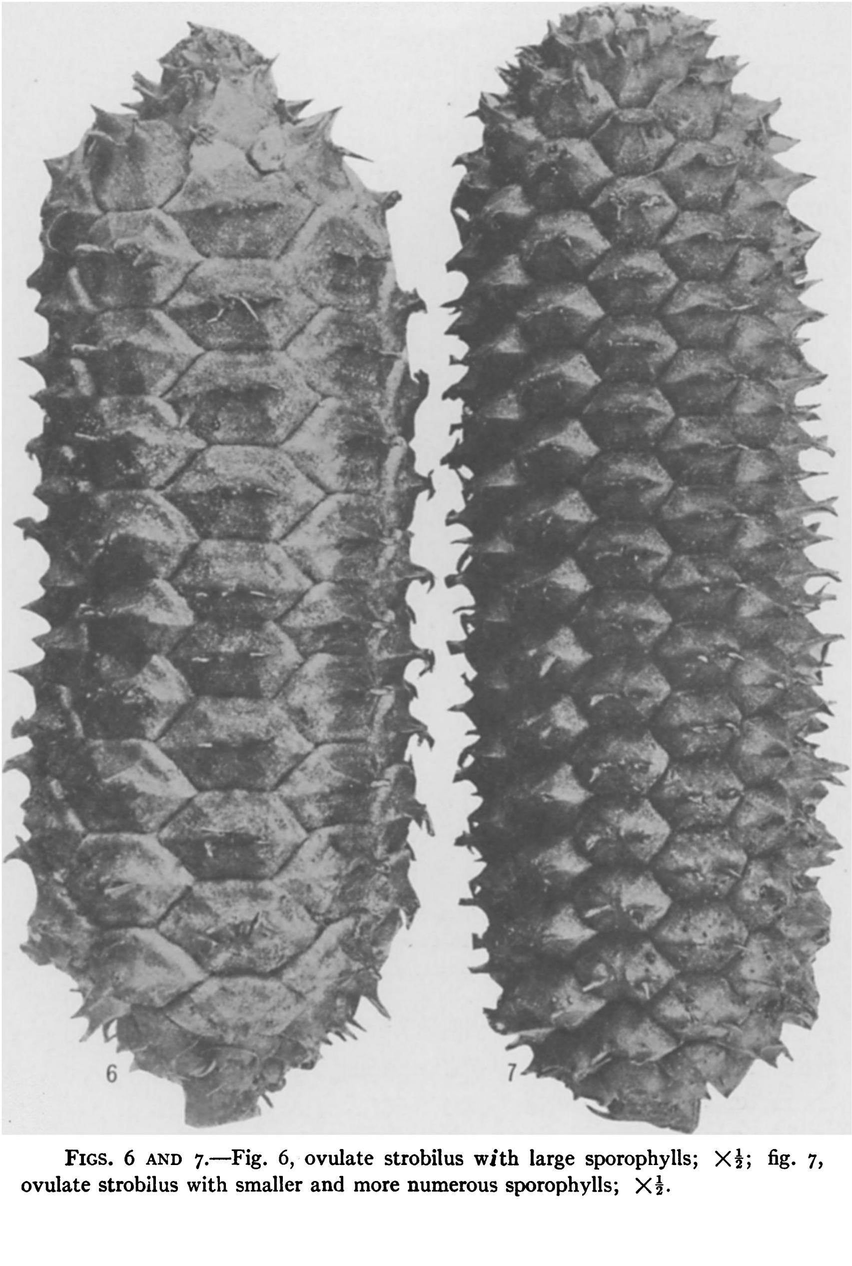
to hold in the hand. At the top of the cone the sporophylls often bear 3 spines and sometimes as many as 5 or 6, the arrangement and vascular connections making it evident that they are reduced pinnae. These sporophylls and some reduced sporophylls at the base of the strobilus bear no ovules.

The young ovules are softly pubescent, but become perfectly smooth at maturity. They are small, seldom reaching more than 2.6 cm. in length and 1.8 cm. in breadth. When very young, and also at maturity, they are white, but during intermediate stages there is a delicate pink color, not very conspicuous from the outside, because the color is in the layer which is to become stony, and consequently is masked by the outer fleshy layer. The stony layer is much thinner than in *Dioon*, and can be cut with a pocket knife, even when the seed is ripe. There is no pit in the base of the stony layer, as in *Dioon edule*, but rather a slight projection, so that the two species can be distinguished from each other by the character of the base of the stony layer.



FIGS. 4 AND 5.—Fig. 4, Transverse section of staminate sporophyll with its sporangia; *m*, mucilage ducts; *v*, vascular bundles; ×10; fig. 5, Portion of wall of microsporangium: *d*, dehiscence; *t*, tapetum; *s*, sporogenous tissue; ×375.

The general distribution of the vascular system of the ovule is as in *Dioon;* in the outer fleshy layer there is a system of unbranched bundles extending from the base of the ovule almost to the micropyle, and in the inner fleshy layer a system of bundles which branch



FIGS. 6 AND 7.—Fig. 6, ovulate strobilus with large sporophylls; $\times\frac{1}{2}$; fig. 7, ovulate strobilus with smaller and more numerous sporophylls; $\times\frac{1}{2}$.

dichotomously and occasionally anastomose. The number of bundles in the outer system varies from 8 to 10, with 9 as the most usual number. About 6 bundles pass through the stony layer to the inner fleshy layer, where they branch repeatedly. In the stalk of the sporophyll there is a single bundle passing toward each ovule; this bundle branches once in the spreading part of the sporophyll, and each branch contributes to both the inner and the outer vascular systems of the ovule.

Both strobili and ovules may reach the maximum size in greenhouse specimens where there has been no possibility of pollination. This seems to be the rule in *Ceratozamia*, although I have seen two or three greenhouse strobili in which nearly all the ovules were abortive.

The male gametophyte

Records in regard to the time of shedding pollen are not very complete. In two staminate cones sent from the Almolongo Valley, near Jalapa, December 5, 1906, arriving in Chicago December 12, the pollen tetrads had already shaken apart, but the exine had not begun to look yellow. In two cones sent from the same place February 5, 1907, and reaching Chicago 7 days later, the pollen was yellow, but the sporangia had not yet dehisced. Four cones from Chiltoyac, near Jalapa, reached Chicago March 10, 1906, and the largest of the four began to shed its pollen 2 days later. A cone of *Ceratozamia mexicana* var. *longifolia*, sent on April 14, 1909, from the Missouri Botanical Garden by Professor Trelease, reached Chicago the following day. Much of the pollen was already shed.

While there is considerable variation in the time at which the pollen is shed, the condition of the pollen at the time of shedding is always the same; there is a tube cell, a well developed, persistent prothallial cell, and a generative cell which will later give rise to the stalk and body cells.

The mature pollen grain of *Ceratozamia mexicana* can be distinguished from that of *Dioon edule* by the spore coats, the exine and intine being quite uniform throughout in *Ceratozamia*, while in *Dioon* the exine is much thicker at the base of the spore and the intine much thickened along the sides.

The pollen grain, as it is shed, is shaped like a kernel of coffee,

with a deep furrow across the top, due to the fact that the exine does not cover the entire surface, but is lacking at the apex of the spore, so that when the spore contracts in the drying out which precedes shedding, the elastic exine springs together until the opposite sides touch, thus making it look as if the exine covered the entire spore. When placed in water or in a nutrient solution, the spore immediately begins to swell, and in a few minutes becomes quite spherical. In a 10 per cent solution of cane sugar, or in the juice of either fresh or preserved pears, germination takes place at once. Within 24 hours the intine begins to protrude, and in 3 or 4 days some of the tubes are two or three times as long as the pollen grain. In cultures there is a considerable elongation of the pollen tube and some increase in the amount of starch, but I have never succeeded in finding a division of the generative cell. The beginning of germination, as it appears in a 10 per cent sugar solution, is shown in figs. 8, 9, and 10.

The pollen tube is quite characteristic, and easily distinguishes *Ceratozamia* from any cycads yet described. As in other cycads, the brown roof of the pollen chamber, with the nucellar beak in its center, is present, but the brown lines due to the haustoria of pollen tubes are scarcely visible, and even in abundantly pollinated strobili the brown spot itself is seldom more than 1 mm. in diameter. That there are haustoria, 2–3 mm. long and lying just beneath the surface of the nucellus, is evident from a glance at a section, but they do not cause conspicuous brown lines upon the surface.

The most striking feature of the pollen tube is a series of secondary haustoria developed from various parts of the enlarged basal end of the pollen tube (fig. 11). As soon as the pollen grain is shed, the primary haustorium, as the familiar haustorium of cycads might be called, begins to develop, and with little or no branching reaches a length of 1–2 mm., its course lying just beneath the surface of the nucellus. The secondary haustoria are developed much later. They have about the same diameter as the primary haustoria, but are more sinuous in outline and usually branch. Their general direction is toward the archegonia, and their development is so rapid that long before the division which is to form the ventral

canal nucleus and egg nucleus, while the archegonial chamber is still quite shallow and the pollen chamber only half way through the nucellus, their tips have already reached the megaspore membrane. They contain starch and occasionally the tube nucleus wanders into one of them, but the tube nucleus, at the stage shown in figs. 11 and 12, is almost invariably found in the enlarged portion of the tube and is usually near the body cell. Only in very early stages is it found in the primary haustorium.

As the tissue of the nucellus breaks down beneath the advancing pollen tubes, the secondary haustoria, especially those extending directly downward, become bent and twisted and finally appear as an irregular tangle pressing against the megaspore membrane (fig. 12). The tissues of the nucellus disorganize so rapidly that the secondary haustoria do not hold back the basal end of the tube, but advance with it. The disorganization which forms the pollen chamber is very extensive, including not only the region occupied by the basal ends of the tubes, but finally all the tissues in the region of the secondary haustoria.

The division of the generative cell into the stalk and body cells, a division which I was not able to secure in cultures, takes place quite promptly after the pollen grains have reached the pollen chamber, probably within a week after pollination. From a record of various cones of various seasons, the time at which the body cell divides shows considerable variation, the division being noted as early as the middle of June, and as late as the first of August. The most usual time is the first week in July.

In nearly all cases, two sperms are produced from each body cell, but four sperms were found in a few cases. In two cases, four sperms were found in isolated pollen tubes mounted without sectioning; in one case, four were found in one tube in serial sections; and in another case, shown in fig. 13, the body cell had divided, forming two cells, each with the aspect of a body cell and with two blepharoplasts, so that there is no doubt as to the manner in which the four sperms are formed.

At the division of the body cell, the mitotic figure is small and entirely intranuclear during the metaphase, but after the nuclear

membrane has broken down in the anaphase, the spindle develops enormously and occupies a broad zone between the two daughter nuclei (fig. 14).

The two cells formed at this division are sperm mother cells, as we have already shown in case of *Dioon edule* (4). In each of the sperm mother cells a sperm is formed, and subsequently escapes by the breaking down of the wall of the mother cell (fig. 15).

The blepharoplast is the largest yet recorded for any cycad, seldom measuring less than 20 μ in diameter, and occasionally reaching a diameter of 27 μ, while blepharoplasts 25 μ in diameter are not rare. The enormous size of this blepharoplast will be appreciated when one remembers that nuclei in the meristematic region of the familiar onion root tip (*Allium Cepa*) seldom measure more than 15 μ in diameter and rarely reach a diameter of 20 μ. Naturally, this blepharoplast is favorable for study, and from the collections of six years the series of stages is very complete, but since such a study should be strictly cytological, I shall reserve for a special paper the division of the body cell and the behavior of the blepharoplast in the formation of the ciliated spiral band. During the formation of the spiral band, remarkable changes take place in the nucleus of the sperm, and these will also be considered in the special paper. For the present, we need only say that the solid blepharoplast becomes vacuolated, and breaks up into a mass of granules from which the greater part of the ciliated band is formed. The band starts in contact with the nucleus, the lowest turn being formed first, and ends at the apex of the sperm. The most usual number of turns of the spiral band is 7, but 6 and also 7.5 are found occasionally. The spiral may be either right or left, or better, it may be formed either in the direction of the hands of a clock or contra clockwise. The actual direction is usually with the hands of the clock, but camera lucida drawings will show the contra clockwise spiral, since the microscopic image is always reversed. In many instances it was possible to determine the direction of the spiral in both of the two sperms from the same body cell, and in most cases one showed the clockwise and the other the contra clockwise direction.

The sperms of *Ceratozamia* are not so large as those of *Zamia* or

Dioon, the average measurements of sperms in the pollen tube being 220 μ in diameter and 185 μ in length from apex to base. The sperms of *Zamia floridana*, as described by WEBBER (5), reach a diameter of 306 μ and a length of 332 μ, and those of *Dioon edule* measure 230 μ in diameter and 300 μ in length. The sperms of *Cycas* and *Microcycas* are smaller.

The sperms were often examined in the living condition. They are easily visible to the naked eye, and with a pocket lens one can see the more general features of their movements, but an examination under low powers of the microscope is more satisfactory. When exposed to the air, the pollen tubes soon burst, the sperms seldom swimming longer than 15 minutes after the ovules are opened, but when the ovules are cut transversely, the female gametophyte removed, and the cut end placed in a drop of sugar solution on a slide, the tubes may be examined for a few seconds at a time and thus allow a more prolonged observation. Just how long the sperms are in the motile condition was not determined, for sperms which have not begun to move when an ovule is opened may suffer from the shock, and when sperms are already moving it cannot be determined how long they have been motile. Movements of individual sperms have been observed for 6 hours.

The movements are like those described for *Dioon edule*, a forward movement accompanied by a rotation upon the axis. The sperms swim rapidly, bumping against each other and against the sides of the tube. When swimming straight ahead the apex is stretched out in front (fig. 16), but when the sperm strikes anything the apex is often drawn in suddenly, with a movement reminding one of the sudden retreat of a *Vorticella*. So far as the form is concerned, the drawings of three sperms shown in figs. 15 and 16 might have been made from a single sperm at intervals of a few seconds. There is also a slower, amoeboid movement of both cytoplasm and nucleus. The contour of the nucleus is very irregular and is constantly changing. Slender prolongations of the nucleus may reach nearly or quite to the ciliated band.

A few attempts were made to determine whether the sperms are chemotactic or not, but no results were obtained. MIYAKE (8) reported that the sperms of *Cycas* show no chemotropism, and

while his results were negative, I am inclined to believe they are entirely correct, for the entrance of the sperm into the egg in both *Ceratozamia* and *Dioon* seems to be independent of any chemotactic phenomena.

The female gametophyte

If strobili were numerous, *Ceratozamia* would be favorable for a study of the origin and development of the megaspore, for the strobili break through the bud scales at a very early stage. The earliest stage in any material shows free nuclear division in the megaspore. The general course of development is about the same as in *Dioon edule* (**9**), the principal differences being that structures are smaller, the mature gametophyte being about 2.5 cm. in length, and the archegonia at the time of fertilization seldom reaching a length of more than 3 mm.

WARMING (**10**) in 1877 reported a ventral canal cell in *Ceratozamia robusta*, but soon concluded that he had been mistaken. It is not surprising that he was in doubt, for the ventral canal nucleus in *Ceratozamia mexicana* is very small and usually disorganizes very promptly. The relative sizes of the ventral canal nucleus and the egg nucleus are shown in fig. 17, while 17*a* is a detailed drawing of the ventral canal nucleus shown in fig. 17. It is of special interest to note that the ventral canal nucleus does not always disorganize, but may enlarge, as it sometimes does in *Pinus* (**11**) and *Ginkgo* (**12**), and in such cases it is very probable that the egg may be fertilized by the ventral canal nucleus. I have seen two cases in *Ceratozamia* in which a large nucleus, looking like the nucleus of the sperm, was only a short distance from the egg nucleus, but no ciliated band could be found in the egg and the neck cells were still turgid. The objection is easily made that the failure to find the ciliated band is only negative evidence, but the band is so large and so persistent, that to one familiar with cycads the failure to find it at this early stage is conclusive proof that no band is present. Of course it might be suggested that only the nucleus had entered the egg, the band remaining outside, but in many cases the sperm, with the ciliated band, was observed inside the egg, sometimes being plainly visible in late free nuclear stages of the proembryo (fig. 20).

A strong reason for believing that fertilization is sometimes effected by a ventral canal nucleus is found in a paper by VAN TIEGHEM (**13**) published in 1870. He secured four seedlings, the result of fertilization of the ovules of *Ceratozamia longifolia* by "the pollen of *C. mexicana*, which had been preserved for three years." VAN TIEGHEM speaks of these seedlings as hybrids, but I do not believe the pollen of *Ceratozamia* will live for three years. Pollen of *C. mexicana*, shed April 22, 1909, in cultures started on that date and also a week later, germinated immediately, but in cultures made a month later from the same collection of pollen, the grains simply became spherical, but would not germinate. In January 1911, I pollinated two cones of *Zamia Ottonis* with some of the same pollen, at about the same time pollinating another cone of *Z. Ottonis* with pollen of *Z. floridana*. I have not yet examined the cones, except to note that they are in fine condition, preferring to wait for the later embryo and seedling stages, if there should be any. At the time of this pollination I again made cultures of the old pollen of *Ceratozamia*, but not a single pollen grain germinated, and recently I repeated the attempt, but no germination occurred. The old pollen is doubtless dead, and VAN TIEGHEM'S seedlings were parthenogenetic or were the result of fertilization by a ventral canal nucleus. I might mention here that I have preparations of *Encephalartos* from a greenhouse specimen where there had been no possibility of pollination, in which the ventral canal nucleus has become greatly enlarged and has moved toward the egg nucleus. I should not be surprised to find occasional seedlings from cycads in greenhouses where there has been no pollination.

The archegonial chamber is conspicuous before the pollen tubes are half way through the nucleus, and during the early stages in its development it contains a fluid, doubtless secreted by the gametophyte, for the megaspore membrane is torn loose from the bottom of the chamber. At the time of fertilization the chamber, although moist, does not contain liquid.

The megaspore membrane is thin, only 2.5–3 μ in thickness. It has about the same structure as in *Dioon edule* (**9**), a comparatively homogenous inner layer beset with an outer layer of irregular club-shaped bodies. These bodies, which in some gymnosperms

are prismatic on account of pressure, are so scattered that they are nearly always round in vertical view (fig. 18).

FERTILIZATION

All observations indicate that fertilization takes place as in *Dioon edule*, the liquid from the pollen tube lowering the turgidity of the neck cells of the archegonium, so that they allow the escape of a portion of the cytoplasm of the upper part of the egg, thus producing a vacuole which draws the sperm into the egg.

In numerous instances the sperms were observed within the egg, occasionally two or three sperms entering the same egg, but in such cases the extra sperms remain at the top of the egg, and the nuclei do not slip out from the cytoplasmic sheath. The actual fusion of the sperm and egg nuclei was not observed, and consequently it cannot be stated at present whether they fuse in the resting condition or behave as in *Pinus*.

Embryo

The extent of the free nuclear period in the development of the embryo was not determined, the latest stage observed being the 256-nucleate stage shown in fig. 19. No stages were found between this and the young embryos with suspensors shown in figs. 20–22.

The membrane of the egg, often with traces of the archegonium jacket clinging to it, persists for a long time. Five such membranes, each with a suspensor coming from its base, are shown in fig. 20. In this case four of the suspensors, each with an embryo at its tip, have united, forming a single suspensor with a single embryo. The other suspensor, with its embryo, advanced only half as far before it ceased to develop. In another case (fig. 21), two suspensors with their embryos have united, and the third, although smaller, has reached about the same length. In another case (fig. 22), all the suspensors and embryos developed separately. These cases are characteristic. A single embryo may be the product of one fertilization or may come from several eggs. In early stages, the young embryos are more or less irregular (fig. 23), but regularity is soon established.

The strobili disorganize and shed their seeds very early, often

before the stage shown in figs. 20–23 is reached, and consequently before the cotyledons have begun to be differentiated. Sister HELEN ANGELA (14), noting this fact and finding traces of vascular tissue which might belong to the missing cotyledon, rotated seeds on a klinostat from the time the seeds were liberated until the embryos were mature. Such seeds showed two cotyledons as in other cycads, so that the single cotyledon of *Ceratozamia*, as it is found in nature, is due to a suppression of one of the cotyledons, doubtless on account of the early liberation of the seeds.

The seeds of *Ceratozamia* germinate as soon as they are ripe, a feature which I have noted in *Dioon edule*, *D. spinulosum*, *Zamia floridana*, *Cycas circinalis*, *Macrozamia Fraseri*, and *Stangeria paradoxa*. Very probably the seeds of all cycads may germinate without any resting period; but seeds of *Ceratozamia*, which had become dry in the laboratory, were planted a year later and germinated readily. Seeds of *Dioon edule* which had been in the laboratory for nearly three years germinated. The most favorable time for germination is that immediately following maturity, for at this time nearly all seeds of both *Ceratozamia* and *Dioon* will germinate, but after a lapse of a few months the proportion of seeds which will germinate steadily diminishes.

Summary

1. *Ceratozamia mexicana* grows best in well shaded mesophytic conditions.

2. Any individual in passing from the seedling to the adult stage shows such a progressive change in its leaves, the leaflets becoming larger, broader, thicker, and more numerous, that descriptions of species based largely upon leaves are open to suspicion.

3. The ovulate strobilus shows considerable variation in the size and number of its sporophylls.

4. In addition to the primary haustorium, a system of secondary haustoria is developed later from the basal portions of the pollen tube. There are regularly two sperms, but occasionally four are produced.

5. A small ventral canal nucleus is present, but occasionally it enlarges and may fertilize the egg. It is suggested that this

may explain the so-called hybrids obtained by VAN TIEGHEM. In most cases fertilization occurs in the usual way.

6. Both suspensors and young embryos may unite, so that from five fertilized eggs there may come one to five embryos. In the mature seed, as found in nature, there is one embryo with a single cotyledon.

THE UNIVERSITY OF CHICAGO

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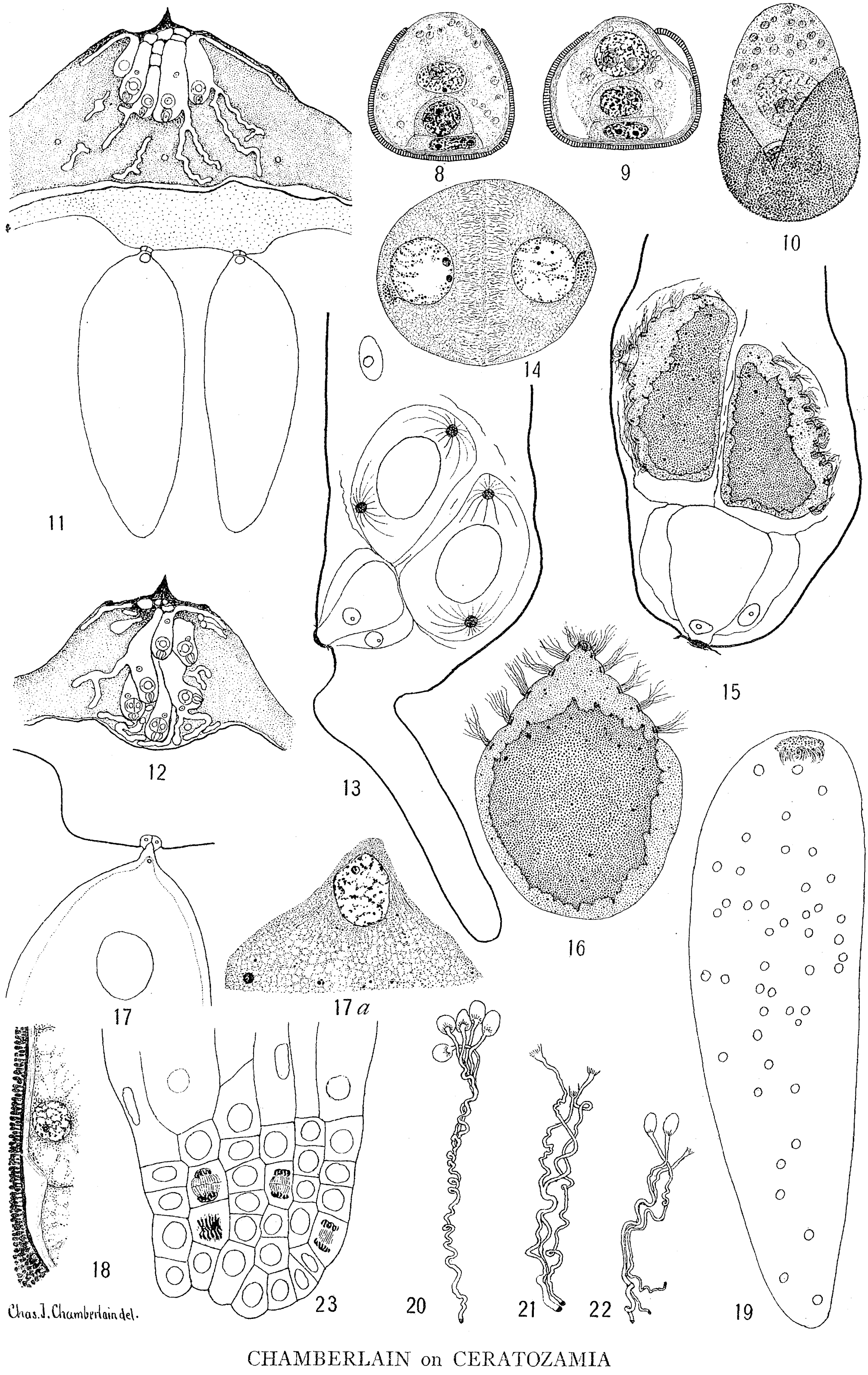

CHAMBERLAIN on CERATOZAMIA

EXPLANATION OF PLATE I

(Figs. 1–7 are text cuts)

Ceratozamia mexicana

FIG. 8.—Pollen grain beginning to germinate in a sugar solution; beneath the tube nucleus is the generative cell which is to produce the stalk and body cells; beneath this and resting upon the intine is the single persistent prothallial cell; the spherical bodies are starch grains; $\times 730$.

FIG. 9.—Like the preceding figure, but there has been some plasmolysis, and at the right side of the figure, toward the top, the intine has pulled loose from the exine; $\times 730$.

FIG. 10.—Germinating pollen grain drawn from living material; $\times 730$.

FIG. 11.—Nucellus and part of female gametophyte with archegonia; the pollen tube at the right shows the primary haustorium just beneath the upper surface of the nucellus, and farther down, opposite the body cell, a branching secondary haustorium; the lightly dotted area above the archegonia represents the liquid filling the archegonial chamber and pressing up the megaspore membrane, represented by the dark line; $\times 14$.

FIG. 12.—Nucellus at a later stage showing behavior of secondary haustoria; $\times 14$.

FIG. 13.—Pollen tube which would have produced four sperms; a single unbranched secondary haustorium extends obliquely downward; $\times 130$.

FIG. 14.—Two young sperm mother cells showing the remnants of the broad spindle and the ciliated band just beginning to form; $\times 180$.

FIG. 15.—Two sperms about to escape from their mother cells; $\times 130$.

FIG. 16.—Mature sperm; $\times 180$.

FIG. 17.—Part of archegonial chamber and upper part of the archegonium, showing the small ventral canal nucleus and the egg nucleus; $\times 25$.

FIG. 17*a*.—Detailed drawing of the ventral canal nucleus shown in the preceding figure; $\times 475$.

FIG. 18.—Megaspore membrane with parts of two adjacent endosperm cells; $\times 833$.

FIG. 19.—Free nuclear stage of proembryo; the sheath and ciliated band of the sperm are shown at the top; $\times 27$.

FIG. 20.—One embryo formed by the fusion of four; the fifth embryo stopped developing part way down the suspensor region; $\times 1.5$.

FIG. 21.—Three suspensors with two embryos; $\times 1.5$.

FIG. 22.—Each suspensor has an embryo at its tip; $\times 1.5$.

FIG. 23.—Young embryo showing irregular outline of an embryo formed by fusion of two or more embryos; $\times 1.5$.